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Host-relations of the Batfly *Megistopoda aranea* (Diptera: Streblidae) in Panamá[1]

William L. Overal[2]

CONTENTS

Abstract

Megistopoda aranea (Coquillett, 1899) is the most common insect ectoparasite of the frugivorous bat *Artibeus jamaicensis* (Chiroptera; Phyllostomatidae) in Panamá. This flightless batfly infests about 60% of individuals of this host species, whereas its occurence on other hosts is sporadic and probably accidental. When these flies are separated from hosts, they survive only 5-20 h. Normally, they never leave the host except when females pupiposit. Puparia are placed in the bat roost in the vicinity of the host, usually on a rough surface above the host. The pupal stadium lasts about 23 days under conditions resembling those in a bat roost. Newly emerged adults can curvive about 36 h before feeding. Copulation was observed to occur two days after emergence. The larval stages which are passed within the female's body total 10 days. Adults of both sexes lived for about two months on caged *A. jamaicensis*. The main source of mortality was host grooming.

M. aranea occupies the host's body fur and avoids the wing membranes. In choice arenas these batflies show a marked preference for rougher surfaces, behavior which is probably important for the maintenance of contact between batflies and their hosts. Increased locomotory activity was observed in response to sudden movements of air. In an "alert" posture the fly raises three legs while standing on its alternate legs. This often precedes a "procession" movement in which the animal moves sideways in an outward spiral on a horizontal surface. Host odor was not found to have attractiveness for *M. aranea,* although temperatures in the range of the host's skin temperature may be attractive.

Megistopoda aranea is probably restricted to *Artibeus jamaicensis* by ecological factors, such as roosting behavior of this host and colony size and stability, in addition to intrinsic factors, such as host odor or physiology.

Introduction

That a host organism and its obligate parasite constitute a unified system, linked by physiological, ecological and behavioral compatabilities, requires that answers to problems of maintenance of the parasitic relationship be sought in the biology of both the host and parasite. The present study seeks to determine how the association between the batfly *Megistopoda aranea*

[1] Contribution no. 1705 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

[2] Present address: Museu Paraense Emílio Goeldi, Caixa Postal 399, 66000 Belém, Pará, Brasil.

(Coquillett, 1899) and its principal host, the Jamaican Fruit-eating Bat, *Artibeus jamaicensis jamaicensis* Leach, is maintained. Aspects of this association which were investigated concern the life history, orientation behavior and occurrence of the batfly, the activities and habits of the host, and the co-existence of the host and parasite.

Like other species of the dipterous family Streblidae, *Megistopoda aranea* is an obligate, blood-sucking parasite of bats. It is reported in the Neotropical Region from Mexico to Brazil, Paraguay and Perú, and throughout the West Indies (Wenzel, 1970). Determination of this species from the United States (Stiles and Nolan, 1931: 658) refers to an accidental introduction or is in error because none of the hosts of *M. aranea* are resident in that country. The batfly has been frequently collected in Panamá and the Canal Zone (Wenzel et al., 1966), where the present study was conducted. Other specimens used in this investigation were collected in Costa Rica and Mexico.

Contributions to our knowledge of the life cycles and natural history of streblids have been made by Muir (1911), Jobling (1949), Ross (1961), and Wenzel et al. (1966). Immature stages have been discussed and figured by several authors (cf. Maa, 1971), and such findings are well summarized by Hennig (1952: 405). The biology of nycteribiid batflies is better known than that of streblids, primarily through the works of Rodhain and Bequaert (1916), Hase (1931), Schulz (1939), Ryberg (1947), Hurka (1964), Leong and Marshall (1968), and Marshall (1970*a*, 1970*b*). Aspects of hippoboscid biology relevant to this study have been presented by Coatney (1931), Bequaert (1953), and Hill (1963). Important questions pertaining to the adaptations and host-specificities of pupiparous Diptera have been raised and discussed by Theodor (1957), and Wenzel and Tipton (1966).

Taxonomic placement of *aranea* in the genus *Megistopoda* Macquart (1852: 332) was by Maa (1965), when the genus to which it had originally been assigned, *Pterellipsis* Coquillett (1899), was placed in synonymy. Both Maa (1965) and Wenzel et al. (1966) indicated that *aranea* may be a junior synonym of the type species of the genus, *Megistopoda pilatei* Macquart (1852). *Megistopoda desiderata* Speiser (1900) is a synonym of *M. aranea* (Coq.) (Aldrich, 1907). The morphology of *M. aranea* has been investigated by Jobling (1949: 316; 1952: 134) and Machado-Allison (1966: 70).

Megistopoda aranea was chosen for this study because of its relative abundance in Panamá and because of the high degree of host specificity indicated by collections (Wenzel et al., 1966). Host bats can be kept in the laboratory (Novick, 1960), and their dietary and roosting habits are known (Goodwin and Greenhall, 1961). The fly is flightless and can be handled without damage. It is easily located on a host due to its size, light tan color, and long hind legs. *Megistopoda aranea* is distinctive and not easily confused with other streblids. Even congeneric species may be distinguished under low magnification. Sexing is easily accomplished with etherized flies. The availability of natural colonies of infested *Artibeus jamaicensis* which could be observed directly permitted the formulation of hypotheses which could be tested with laboratory colonies of the host and parasite.

Materials and Methods

Field work was done in the Republic of Panamá and the Canal Zone during December, 1970, and January, June, July and August, 1971. Laboratory work was done at the field station of the Smithsonian Tropical Research Institute on

Barro Colorado Island in the Canal Zone and at the Department of Entomology of the University of Kansas.

Bats and batflies were caught in Panamá or the Canal Zone with the use of nets. Mist nets were employed in the manner illustrated by Greenhall and Paradiso (1968), usually being placed over streams, along forest trails, or under fruiting fig trees known to be attractive to *Artibeus* bats. Within caves or buildings containing bat roosts, hand nets were used. In either case bats were placed individually in paper bags for transport to the laboratory or before being etherized, to avoid the misassociation of their parasites. *Artibeus jamaicensis* has been reported as a carrier of rabies virus in Panamá (Constantine, 1970: 355; Keenan, pers. comm.). Because infected bats can transmit rabies to man, all bats were handled with gloves by personnel vaccinated with duck embryo rabies vaccine.

Batflies were removed with forceps from the bat or from the paper bag in which a bat was kept. Catching the flies by their hind legs did not appear to cripple them or affect their behavior. Live flies were kept on a host until use. Dead flies were preserved in 70% ethanol, and hosts were preserved in formalin for identification.

Bats used in experimental infestations were housed in shaded areas outside the laboratory on Barro Colorado Island, in cages of 0.6 cm wire mesh. Although the batflies could easily pass through this screening, this was not found to be a source of batfly losses since the flies remained in contact with a host and did not wander off. Cages were cylindrical, 60 cm high and 45 cm diameter, with a detachable bottom for convenience in cleaning. Generally, no more than 12 bats were kept in a cage of this size. A flight cage (10 m $\times$ 5 m $\times$ 3 m) with a concrete floor was used to house a colony of 155 bats.

The experimental bats, *A. jamaicensis* and other stenodermines, are frugivorous and can be maintained on diets of fruits and vitamin supplements. Fruits accepted by *A. jamaicensis* include bananas, figs, mangoes, melons and apples. These were peeled, sliced, and mixed with dried milk powder and vitamin syrup. Water was continuously available to the bats, but none was observed to drink. The environmental conditions under which the bats were kept varied more than did the conditions in bat roosts from which some bats were collected, but this did not appear to have a significant effect on the bats. The temperature varied from 16°C to 30°C and the relative humidity from 60% to saturation in a daily pattern (Fig. 1). Individual bats in the laboratory colony were marked by application of quick-drying paints to their hind claws which permitted identification from outside the cage.

In addition to laboratory colonies, natural colonies of *A. jamaicensis* were observed in their roosts for comparative purposes. These colonies were located in three abandoned bunkers in Ft. Kobbe, C.Z., in Chilibrillo Caves, Chilibre, Panamá, and in a culvert under Madden Forest Road, C.Z. Care was taken not to disrupt these colonies, and since individuals were not repeatedly observed, these bats were not banded or marked.

Collections were made of bats and their parasites at several localities in order to survey the geographic distribution of *M. aranea* in Panamá and its incidence and frequency of ocurrence on various hosts. Where possible, a sample of at least 25 *Artibeus jamaicensis* was taken at each locality in order to assess the effect of edaphic conditions on the host-parasite relationship. Those localities where this was possible are listed in Table 1 and mapped in Figure 2. Bats for experimental work were netted in June and July, 1971, at Balboa Heights, C.Z., under a fig tree

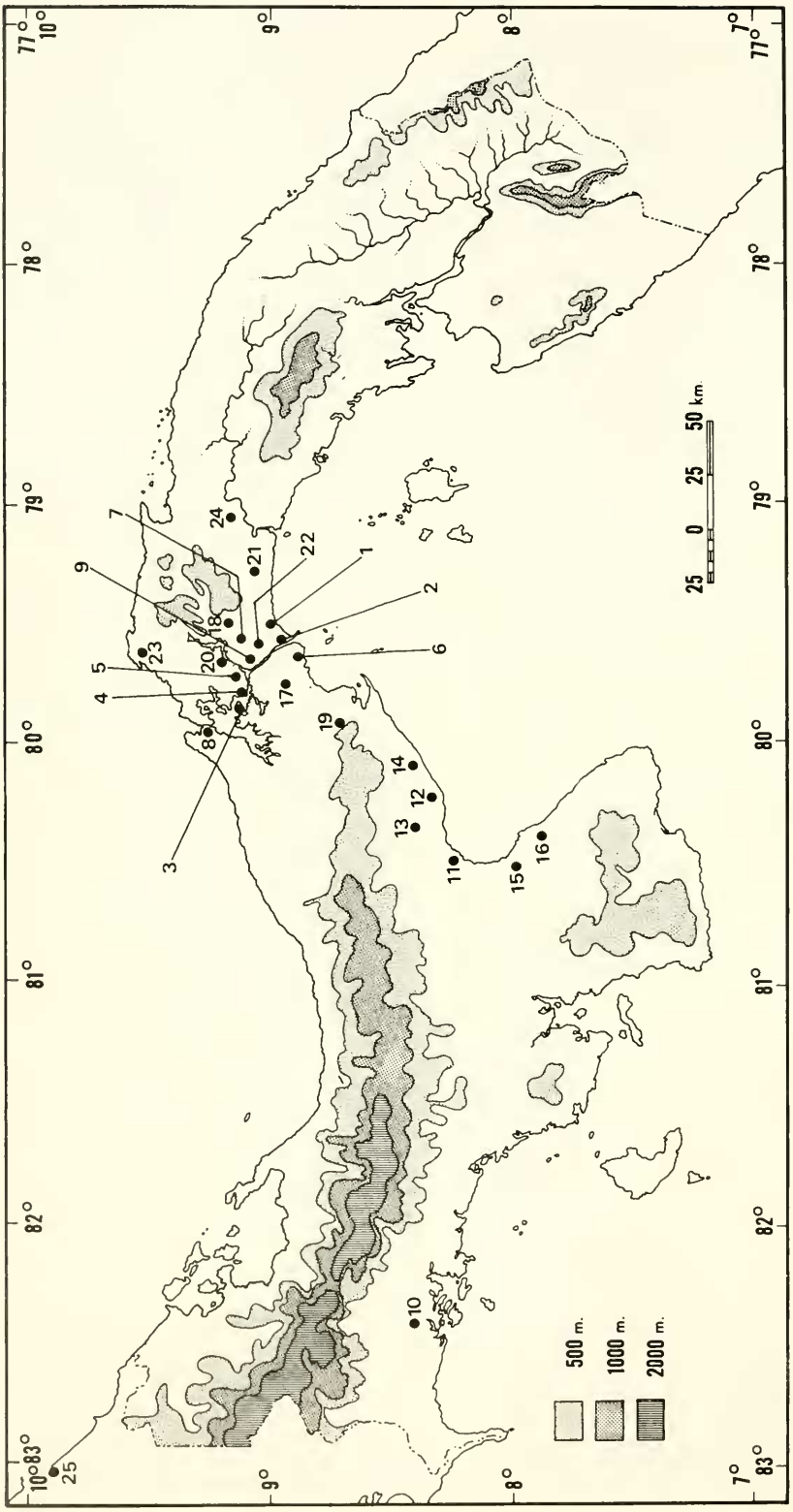

FIG. 1. Temperature and relative humidity in the outdoor bat cage on Barro Colorado Island where experimental animals were maintained; curves averaged over July and August, 1971.

near the railroad station, and at Summit Gardens (Botanical Park), C.Z. Voucher specimens have been deposited with the Museum at Kearney State College, Nebraska (Alcoholic Mammal Collection, Catalog Nos. 1246-1271) in the care of Dr. J. Farney, who verified identifications made in the field. Specimens of *M. aranea* used in this study have been given to the Snow Entomological Museum of the University of Kansas.

Specific techniques relating to the care and use of batflies in behavioral and physiological experiments are presented in the pertinent sections below. Statistical tests are as given by Sokal and Rohlf (1969).

Survey Results

Megistopoda aranea has been reported from a variety of hosts. Reports include *Phyllostomus* sp. (Stiles and Nolan, 1931: 658), *Artibeus yucatanicus* in Mexico (Hoffmann, 1953), *Artibeus planirostris polax* in British Guiana, *Artibeus planirostris trinitatis* in Trinidad and Tobago (Machado-Allison, 1966; Goodwin and

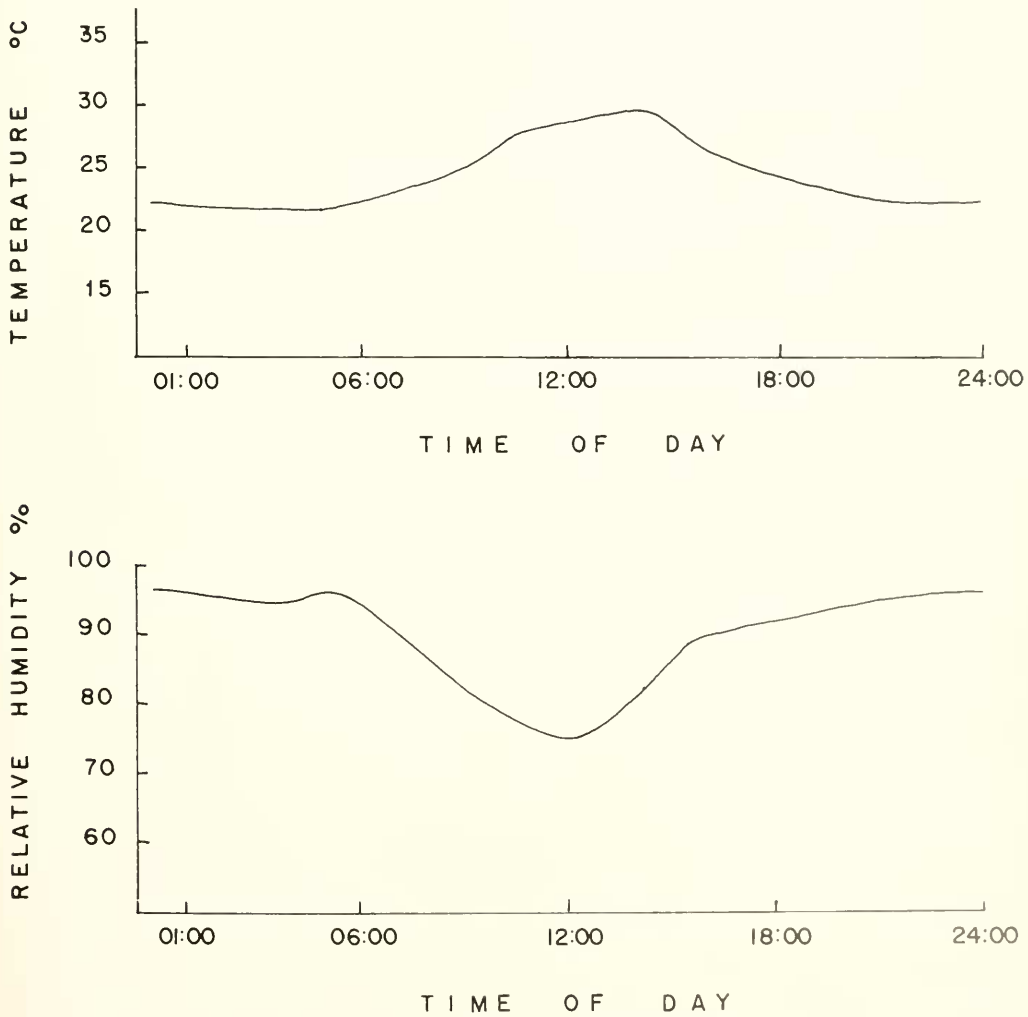

FIG. 2. Map of Panamá showing localities where bats and their parasites were collected. Place names and coordinates for these localities are given in Table 1.

Greenhall, 1961), *Artibeus jamaicensis parvipes* in Cuba (Matheson, 1928), *Sturnira ludovici* in Costa Rica (Tonn and Arnold, 1963), *Artibeus j. jamaicensis, A. literatus palmarum, Carollia perspicillata azteca, Desmodus rotundus murinus,* and *Phyllostomus discolor* in Panamá (Wenzel et al., 1966). The published host records are difficult to interpret because of the unsettled and specialized nature of bat taxonomy and because of the possibilities for errors in associating hosts and parasites during collecting or labeling. Wenzel et al. (1966) believe *Artibeus jamaicensis* and *A. literatus* are the primary hosts of *M. aranea* in Panamá, although *A. literatus,* as interpreted by them, may represent a species complex (Wenzel, pers. comm.).

Examination of collected lots of 14 bat species in Panamá revealed that *M. aranea* was apparently restricted to three species, *Artibeus jamaicensis, A. literatus,* and *Carollia perspicillata.* Figure 3 shows the percentage of each of these species which was infested with *M. aranea. Carollia perspicillata* is probably not a normal host of *M. aranea* because of its low frequency of parasitization and because no *C. perspicillata* had more than one individual of *M. aranea,* suggesting a random transfer. The status of *A. literatus* as a host of *M. aranea* is uncertain. *A. literatus* and *A. jamaicensis* have been netted in the same collection lot, suggesting that they may forage together, but they have not been observed to roost together. They do, however, share the same caves in Panamá, such as the Chilibrillo Caves, and the possibility that *M. aranea* on *A. literatus* may have dispersed, if only temporarily, from *A. jamaicensis* cannot be ruled out.

Of the several previously reported Panamanian hosts of *M. aranea,* only the vampire, *Desmodus rotundus,* was not adequately sampled. More than 200 vampire bats have subsequently been collected from the states of Veracruz, Oaxaca and Chiapas in Mexico, however, and *M.*

TABLE 1. Names and coordinates of localities mapped in Figure 2.

No.	Name	Coordinates[1]	Description
1	Ancon, C.Z.	8°57′N-79°34′W	under fig tree
2	Balboa Heights, C.Z.	8°57′N-79°34′W	under fig tree
3	Barro Colorado Is., C.Z.	9°09′N-79°51′W	forest clearing
4	Frijoles, C.Z.	9°10′N-79°49′W	forest trail
5	Gamboa, C.Z.	9°06′N-79°42′W	under fig tree
6	Ft. Kobbe, C.Z.	8°54′N-79°36′W	abandoned bunker
7	Madden Forest, C.Z.	9°05′N-79°39′W	forest clearing
8	Ft. Sherman, C.Z.	9°21′N-79°57′W	wet forest
9	Summit, C.Z.	9°03′N-79°40′W	Botanical Park
10	David, Chiriqui	8°26′N-82°26′W	near stream
11	Aguadulce, Cocle	8°14′N-80°33′W	forest near docks
12	Anton, Cocle	8°24′N-80°16′W	under fig tree
13	Penonome, Cocle	8°31′N-80°22′W	near Rio Zarati
14	Rio Hato, Cocle	8°22′N-80°16′W	near shore
15	Parita, Herrera	7°59′N-80°32′W	forest boundary
16	Los Santos, Herrera	7°45′N-80°21′W	under fig tree
17	Arraijan, Panamá	8°57′N-79°41′W	forest near C.Z.
18	Calzada Larga, Panamá	9°10′N-79°34′W	abandoned bunkers
19	Cerro Campana, Panamá	8°41′N-79°56′W	cloud forest
20	Chilibre, Panamá	9°08′N-79°38′W	Chilibrillo Caves
21	Pacora, Panamá	9°04′N-79°18′W	under fig tree
22	Panama (city), Panamá	8°58′N-79°32′W	under fig tree
23	Portobello, Colon	9°41′N-79°41′W	forest trail
24	Chepo, Darien	9°10′N-79°06′W	forest
25	Limon, Costa Rica	9°58′N-83°08′W	coffee finca

[1] Coordinates were compiled from several maps and from Fairchild and Handley (1966).

aranea has not been found associated with any of them. *M. aranea* is found in these areas on *Artibeus,* and its absence from *Desmodus* is significant.

The results of the survey confirm the statement by Wenzel et al. (1966) that "this species appears to be a parasite primarily of *Artibeus jamaicensis*" and secondarily of *A. literatus* in Panamá. Caution should be exercised in extrapolating these results to areas outside Panamá, but collections made in Costa Rica and tropical Mexico indicate that subspecies of *A. jamaicensis* are the primary hosts of *M. aranea* in these countries also. Collections in the care of Dr. Wenzel (pers. comm.) show this to be true also in Venezuela, Surinam, Colombia and San Salvador. *Megistopoda aranea* can be considered monoxenous or, perhaps, oligoxenous.

Field collections can shed light on the behavioral aspects of host selection. No difference was found in the average infestation levels between males and females of *Artibeus jamaicensis,* indicating that the fly may not discriminate between the sexes of its host. This was confirmed in the laboratory with choice tests. The frequency distribution of infestation of *M. aranea* on *A. jamaicensis* follows the expected Poisson (random) distribution (Table 2 and Fig. 4), indicating that the flies do not preferentially segregate with one another and that hosts are nearly alike in their attractiveness. The frequencies of occurrence of both male and female flies on the same host are not significantly different from the expected frequencies, and it may be assumed that flies do not pair with flies of the opposite sex in host selection, in contrast to the situation noted by Hurka (1964) in several European nycteribiids. No correlation of the parasite load with the weight or forearm length of the host was found in a sample of 85 bats.

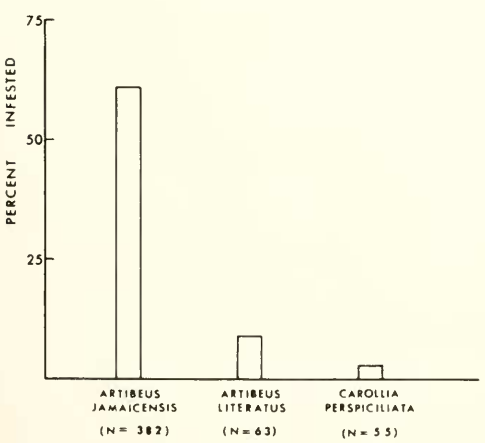

FIG. 3. Frequencies of infestation of *Megistopoda aranea* on three bats species in the Canal Zone.

Although the parasite is buffered from changes in environment by the homeostasis of the host, there were slight differences in the average infestations of *Artibeus jamaicensis* between the wet and dry seasons of 1971. Sixty-two bats caught during the wet season had an average of 0.843 flies per host, compared with 0.611 flies per host found on 57 bats caught during the dry season. That these differences could reflect a direct effect of climate on the parasite is only one possibility. It is also likely that there is an effect on the host, reflected in some significant alteration in its biology. Mares and Wilson (1971) have found a marked seasonality in the breeding cycle of several neotropical bats. Whether such a condition could influence roost selection or sociality of the bats, in such a way that the host-parasite equilibrium would be disturbed, has yet to be explored.

Observations on colonies of *Artibeus jamaicensis* in natural and man-made roosts indicate how the dynamics of host populations may affect the population levels of *Megistopoda aranea.* In several situations bats roosted in close proximity to one another and the fur over which flies moved was effectively continuous from bat to bat. Host-to-host dispersal by this means was suspected and later confirmed. If the

proximity of roosting bats in a colony is assumed as an index of sociality, the possible relationship of sociality to parasitism by *Megistopoda aranea* becomes clearer; dispersal to new hosts becomes dependent upon the sociality of the host. Colony size may also be important for the presence or absence of the parasite, since smaller colonies may not provide sufficient refuge from the grooming activities of individual hosts. While there are no data to support this conjecture, it remains of interest for further investigation.

LIFE CYCLE OF *Megistopoda aranea*

The free-living, non-parasitic stages of *Megistopoda aranea* are reduced, as is the case throughout the Pupipara. The larval stadia last ten days, based on the minimum time between successive pupal depositions by the same female. During this period the larva is nourished in the female by a uterine gland secretion (Hagan, 1951) and is only indirectly dependent upon a host bat. Attempts to demonstrate that gravid females ingested more blood than non-gravid females were inconclusive, and future investigations along these lines may require radioactive tracers to determine the amount of blood ingested. A gravid female ready to expel the prepupa can be distinguished by the degree of enlargement of its abdomen. Such females were removed from hosts and placed in stoppered vials for the collection of puparia.

Within 10 min of its deposition, the

TABLE 2. Frequencies of absence and single and multiple occurrences of *Megistopoda aranea* on *Artibeus jamaicensis*. Expected frequencies are based on a sex ratio of 1 male:1.25 females and a Poisson distribution where the average is 0.843 flies per host for 412 hosts. All hosts were caught in the Canal Zone during June and July of 1971.

No. of flies	Sexes of flies	Observed frequency		Expected frequency	
0	....	....	188	....	177.3
1	1♂	74	133	66.4	149.5
	1♀	86		83.1	
2	2♂	17	68	12.4	63.0
	1♂1♀	27		31.1	
	2♀	24		19.5	
3	3♂	2	18	1.6	17.7
	1♂2♀	5		5.8	
	2♂1♀	10		7.3	
	3♀	1		3.0	
4	4♂	0	3	0.15	3.73
	1♂3♀	1		0.73	
	2♂2♀	1		1.36	
	3♂1♀	0		1.14	
	4♀	1		0.35	
5	....	0	0	....	0.63
6	6♂	0	2	0.001	0.09
	1♂5♀	0		0.006	
	2♂4♀	0		0.017	
	3♂3♀	1		0.026	
	4♂2♀	1		0.024	
	5♂1♀	0		0.013	
	6♀	0		0.003	

Observed and expected frequencies are not significantly different. (Chi-squared test.)

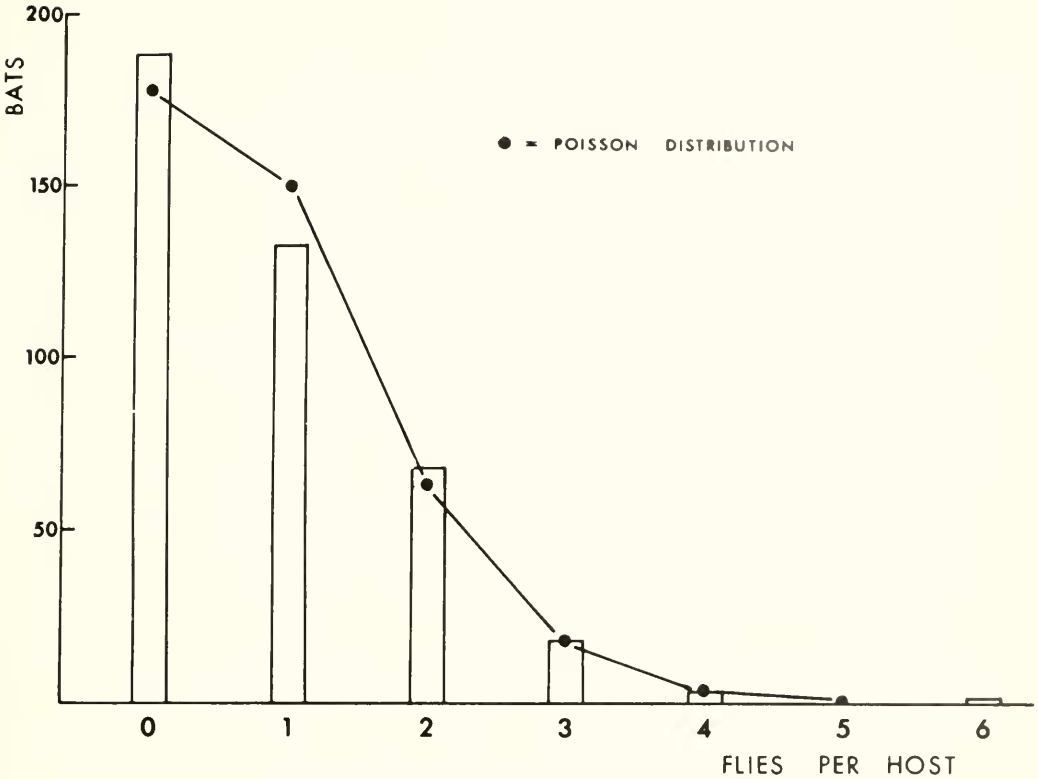

FIG. 4. Frequencies of occurrence of *Megistopoda aranea* on *Artibeus jamaicensis*.

subglobose larva darkens from a transparent colorless form to a brown puparium with evident segmentation. The ventral surface of puparia deposited on glass did not darken, suggesting that the process depends upon contact with air. In addition to the protection afforded it by the toughened larval cuticle, the larva is usually deposited in an indentation. The actual orientation of the puparium does not appear to be important, and both vertical and horizontal surfaces were selected by *M. aranea* for larval deposition. A characteristic place in a stoppered vial was on the glass between the cork and the wall of the vial. In natural colonies of *Artibeus jamaicensis,* puparia were found in areas above the roosting bats. This pupa-position site differs from that of fully winged streblids which may deposit pupae in areas quite removed from the roosting bats, as in a different chamber of a cave, and from that of hippoboscids which may deposit pupae loosely in nesting materials or on the host itself. This last case is not a possibility for *M. aranea,* however, because of the frequent and vigorous grooming by the host and the long developmental period of the pupa.

The pupal stadium lasted 22 to 24 days at 100% R.H. and approximately 22°C. The mean developmental time for 25 pupae was 23 days. The puparium has two posterior spiracles and an oblong base by which it is attached to the substrate (see Hennig, 1952). The dimensions of 25 puparia of *M. aranea* averaged as follows: length—1.6 mm; width—1.1 mm; height —0.8 mm. The teneral adult emerges through an anterior operculum and remains near the empty puparium for several hours. Table 3 shows the survival times of unfed teneral adults. The teneral fly is readily distinguished by its pale color

and crenulate abdomen. A ptilinum was not noted in newly emerged flies.

As observed by Ross (1961) in Arizona, teneral individuals of *Trichobius* spp. cannot mate until they have fed, probably because of the deformation or small size of the abdomen which may be mechanically incapable of copulation. This could apply to *M. aranea* also because no unfed teneral flies were observed to mate. Mating occurs on the host bat and usually lasts one to five minutes. Females were sometimes seen to mate only a few minutes after depositing a pupa.

The presence of both sexes in nearly equal numbers (Table 3) suggests that mating is required for reproduction and that the storage of sperm by the female, if it occurs, is of little importance. Since six adult females separated from males produced maximally only one pupa each during the following three weeks and females which had never been kept with males produced none, a separate mating is probably required for each offspring produced.

Attempts to mark individual flies for life-history studies were unsuccessful due to an apparent toxicity of the oil- and lacquer-based paints which were employed, and measurements of longevity and fecundity are therefore indirect. To measure longevity, newly enclosed *M. aranea* were placed on ten caged *Artibeus jamaicensis* hosts. The flies were counted at weekly intervals (Fig. 5) until the last fly had died or been lost. The average lifespan of these 40 flies was 29 days, and the survivorship curve indicates that the bulk of the mortality was due to sources other than old age. Thirteen dead and damaged flies were recovered from the bottom of the bat cage. Certainly, both the grooming of the host (possibly involving predation) and disassociation from a host should be considered as major causes of mortality. Adults of *M. aranea* were accepted and eaten by *A. jamaicensis* when offered in the laboratory. D. Howell (pers. comm.) has found streblids in the stomachs of several species of Costa Rican bats. An acarine parasite of *M. aranea* adults, *Monunguis streblida* Wharton (Wharton, 1938; Linquist and Vercammen-Grandjean, 1971), has been reported, but no hyperparasites were seen during this study.

Pupal mortality was measured as the percentage of puparia which did not give rise to adults by the end of four weeks. Puparia were deposited on a piece of plywood on top of the outdoor bat cage over the dark corner in which the bats roosted. The board was then removed to the top of an empty cage, and the puparia were examined at the end of a month. Twelve per cent of the puparia (23 of 192) had not given rise to adults, although no reason for their failure could be seen. Two puparia had been damaged (probably in relocating the board) and had been attacked by fungus. The survival of pupae may be assumed to be a function of en-

TABLE 3. Survival times of *Megistopoda aranea* separated from hosts. Both adults which had been allowed to engorge and unfed, newly eclosed tenerals were kept at 100% R.H. and 22°C.

Survival times of engorged adult flies (in hours)	Survival times of unfed teneral flies (in hours)
3	18
5	26
8	36
14	38+
17	
19	
20	

Tenerals survived significantly longer than engorged adults. ($P<.05$) Mann-Whitney-*U* test.)

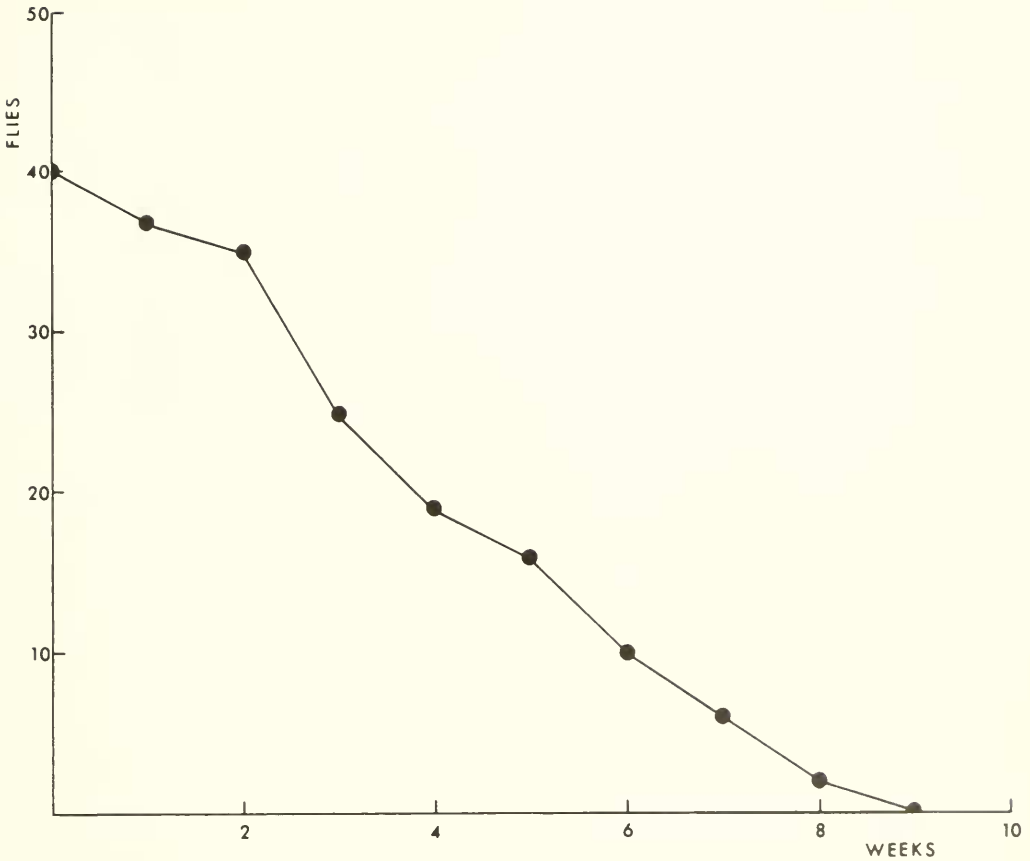

FIG. 5. Survivorship of *Megistopoda aranea* on ten caged *Artibeus jamaicensis*.

vironmental conditions. The present observations, therefore, may reflect more upon the conditions provided for pupal development than on the usual successes of the pupal stage.

In Chilibrillo Caves and in bunkers at Ft. Kobbe, puparia which resembled those of *M. aranea* were found in proximity to colonies of *Artibeus jamaicensis*. Those removed at random in various seasons from the roosts were in a variety of developmental stages, suggesting that reproduction by the bat fly is asynchronous and continuous. The cave and bunker were similar environments with moderate temperatures and a relative humidity near saturation, but colonies of *Artibeus jamaicensis* were also observed in foliage and in a hollow tree where conditions were much different. Pupae in the laboratory developed at 18°C and those in outdoor bat cages at temperatures 21 to 30°C, indicating that unsheltered colonies, if sufficiently permanent, may be parasitized by *M. aranea*.

Life history observations on *M. aranea* indicate a low reproductive potential. Ignoring larval and pupal mortality and assuming adult age-specific fecundities to be equal, the assembled observations would indicate a net reproductive rate, R_o, of 1.45,

where $R_o = \sum_x^x l_x m_x$, l_x is survivorship and m_x is age-specific fecundity. This figure, while derived from data which may include the effects of predation and sub-

optimal conditions, indicates that a population of *M. aranea* would multiply 1.45 times in a generation, while under optimal conditions a greater net reproductive rate would be expected. It seems reasonable to assume that under natural conditions *M. aranea* populations are stable in the long run, although locally there may be extinctions, probably followed by reintroductions and population growth. The low reproductive potential of *M. aranea* follows from its breeding biology which limits a single female to producing maximally one pupa every ten days.

BEHAVIOR OF *Megistopoda aranea*

The dominant aspects of the behavior of *Megistopoda aranea* are its blood-sucking habit and its dependence upon a host. Flies removed from hosts (Table 3) survive for only a short time, in contrast to other groups of ectoparasites which may remain apart from a host for months. *Megistopoda aranea,* therefore, is found in contact with a host during all adult activities with the exception of pupal deposition, which generally occurs close to a resting host during the day. In the terminology of Camin (1963), *M. aranea* can be said to be a "permanent" ectoparasite.

On its host *Megistopoda aranea* can be found on the furred parts of the body, but prefers sites around the neck and shoulders where the fur is long and in the axillary regions below the wings. When disturbed, flies often run into the bat's ears. The fly moves on the host's fur by pushing itself with alternating extensions of the long hind legs. The thoracic sternum is flat and sled-like, and the first two pairs of legs articulate to the sides. The fly can move with facility over the host pelage with its thorax at the level of the longer guard hairs and is capable of moving forward, backward, or to the side. No fly was observed to jump.

During host grooming, *Megistopoda aranea* was seen to retreat to the lower back of its host to a position just anterior to the uropatagium. This portion of its body could not be reached by the host, which groomed itself with its hind claws, thumb and mouth. Host bats were not observed to groom one another as do some birds. Although no pathological lesions were observed at the feeding sites of *M. aranea,* infested *Artibeus* bats were observed to groom more intensively and frequently when the parasite load was experimentally increased. Flies rarely went onto the wings of the host and would not remain on newly born *A. jamaicensis,* which are hairless, suggesting that thigmotaxis is important in host-recognition. This hypothesis was tested by offering flies a choice of substrates in a closed arena; the results are shown in Table 4. Flies consistently chose rougher substrates. Tactile stimuli are probably important in the fly's maintenance of contact with its host.

Megistopoda aranea and other streblids do not engorge, but feed intermittently throughout the day. It is possible that more feeding is done during the daylight hours when the bats are roosting. This is based upon the frequency of defecation by the fly (Fig. 6). Feces were collected on paper at the bottom of a cage containing one *Artibeus jamaicensis* and five *M. aranea.* The higher daytime feeding rates may be induced by a greater rate of desiccation at the lower relative humidity present during the day, or they may be an adaptation to the resting habits of the host during the day. Favored areas for feeding on the host are around the ears and neck and in the axillary regions. Dissections showed that flies apparently ingest whole blood and do not concentrate blood cells. A liquid fecal drop is produced. Although no volumetric measure of the amount of blood ingested by a fly during a day was possible, it remains a possibility that sev-

eral flies could seriously affect the health of their host.

Megistopoda aranea does not appear to bite humans as do some species of *Trichobius* (Ross, 1961). Flies were frequently handled and in two cases given access for several hours to the upper arm of the investigator, but they did not bite. No animals other than bats were accepted as hosts; mice and rats were rejected and flies placed on them left or died. The texture, odor and temperature of the host may be signal stimuli or feeding stimuli to the fly.

Although *Megistopoda aranea* does not normally leave the body fur of its host except for pupal deposition, flies which have been removed from their hosts exhibit search behavior. Placed on a horizontal pane of glass under diffuse light, such a fly would move in a random fashion for several minutes before assuming an "alert" position in which it would stand on its fore- and hind-leg of one side and its mid-leg of the other side. This position was observed in over 50 flies. The legs not used to support the body were extended above the body and waved about. This behavior suggests that tarsal receptors such as those of the Nycteribiidae, or some other type of sensory organ, may be present on the legs of *M. aranea* (Maa, 1971). This stance may also be adaptive for grasping hosts moving nearby. The fly can be made to abandon its "alert" stance and move rapidly if a sudden air current is directed at it, even in the absence of host odor, as from an empty syringe. The fly will turn toward the source of the air current and run forward for several seconds or until the air current is stopped. Such behavior may be adaptive if a potential host were to cause an air current.

In a second type of "search" pattern seen repeatedly in flies removed from hosts to a horizontal surface, the fly moves sideways in a spiral, halting at intervals to raise one or more legs. How effective either of these "search" patterns would be in the more complex environment of a bat roost is not known.

In a "T-tube" apparatus with an internal diameter of about 8 mm, flies were seen to encounter, turn and walk against the flow of air (22 of 25 flies, $P < .05$, Chi-squared test). This may be related to their response to a current of air when standing still.

TABLE 4. Preferences of *Megistopoda aranea* for type of substrate. Fifteen flies (five at a time) were placed in a petri dish with two substrate types, each covering half of the arena, and were allowed to move freely for 20 min before their selection was recorded. Comparisons were made using the Mann-Whitney-*U* test. (*=$P<.05$)

Test no.	Materials as substrates	Trial A	Trial B	Trial C	Preferred material
1	Glass	0	1	0	
	Paper	5	4	5	*
2	Glass	0	0	0	
	Cotton cloth	5	5	5	*
3	Paper	4	3	5	
	Cloth	1	3	5	ns
4	Water	0	0	0	
	Glass	5	5	5	*
5	Moist towel	0	3	1	
	Glass	5	2	4	ns
6	Cotton	0	1	0	
	Bat fur	5	4	5	*
7	Wet bat fur	0	1	0	
	Dry bat fur	5	4	5	*

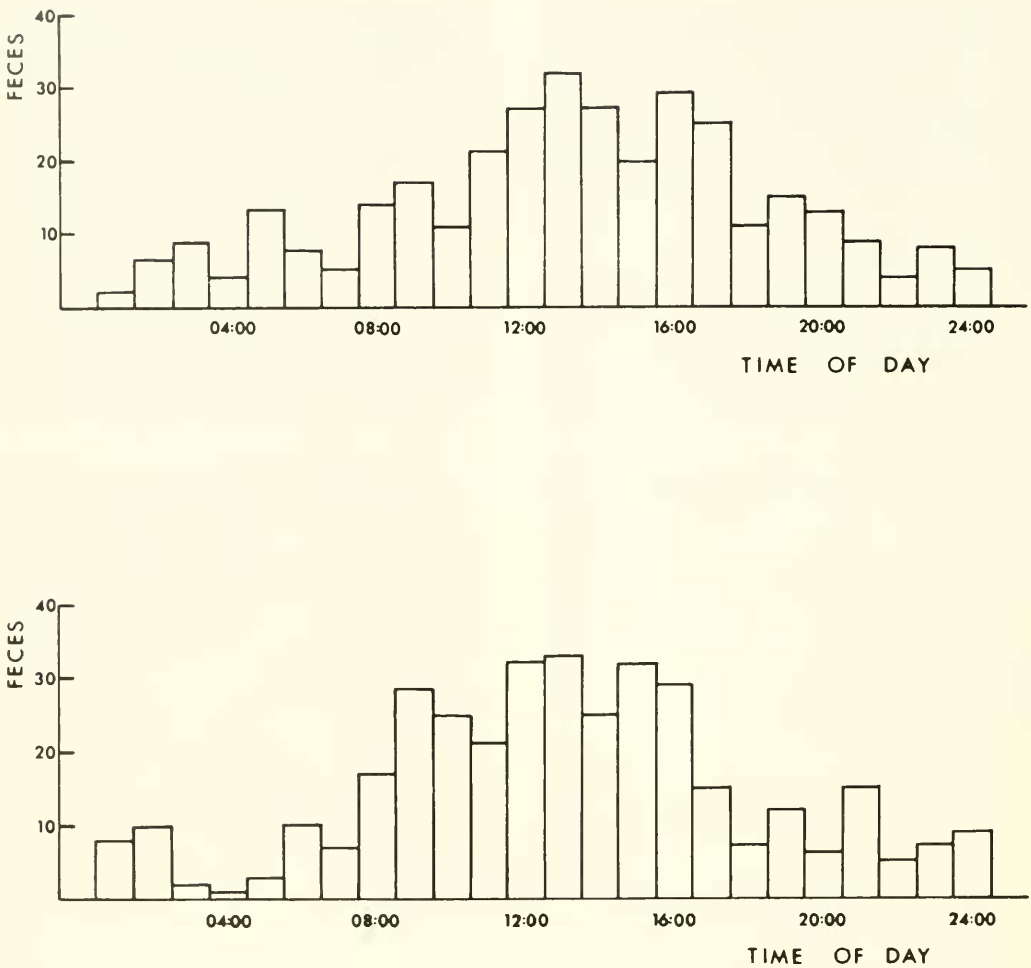

FIG. 6. Defecation rate of five feeding *Megistopoda aranea* during a 48-hour period.

Table 5 shows the results of chemosensory tests using a "T-tube" in which the various stimuli were allowed to diffuse from one end of the "T" for one-half hour before the flies were introduced into the stem. None of the stimuli was shown to have a marked attraction or other effect except the commercial insect repellent. This indicates that, while some olfaction is present, it may not be used in host-finding. This could be expected since the environment of the bat fly is probably saturated with the host odor, and no gradient of odor could be followed to find the host bat over the short distances the flies walk from their hosts.

Host temperature is a valid clue for many ectoparasites in host-recognition and host-finding over small distances. It may also be a feeding stimulus. It appears that *M. aranea* is sensitive to substrate temperature (Table 6). Flies consistently aggregated in the area of a temperature gradient which was between 33 and 38°C. This temperature range includes the body fur temperature of resting *Artibeus jamaicensis* which was measured with a "banjo" probe and a Yellow Spring Instrument

Company tele-thermometer. These bats had a surface temperature of 32° ± 2°C, but temperatures rose rapidly as the bat struggled to free itself or bit the thermistor probe. Bats generally have fluctuating body temperature, and many resting bats allow their temperature to rise or drop to the ambient temperature (Henshaw, 1970). *Artibeus* bats were not tested in an unstressed condition, and it is not known if this is true for them. Only to the extent that their temperature remains above ambient can temperature preference be dependable for host-finding by their parasites.

Host-finding is initially important to *Megistopoda aranea* of both sexes after eclosion. The teneral adult can survive longer without a host than can a fed adult (Table 3). This result agrees with the findings of Marshall (1970*a*) and Leong and Marshall (1968) for two nycteribiid species. The initial advantage is probably greater for *M. aranea,* however, because no host-associated stimulus for eclosion seems to be involved which would indicate the presence of a host, such as has been reported for *Basilia hispida* (Nycteribiidae) (Marshall, 1970*a*, 1970*b*). Even if such a stimulus were present, the roosting sites of *Artibeus* are shared with other species, and the bat which may trigger eclosion could be one of a number of stenodermine or other bats. No doubt newly emerged flies could get onto irregular hosts which have replaced an *Artibeus* colony.

Flies did not select a particular relative humidity in a gradient, nor were they excited or stimulated to move by low concentrations of carbon-dioxide in the air. They did not preferentially select either light or dark areas in an arena, and their distribution in a vertical cylinder was without regard to gravity. *Megistopoda aranea,* like other streblids, can walk upside-down on glass and could even adopt the "alert" stance in this orientation.

Table 7 indicates that *Megistopoda aranea* has the ability to discriminate between host species that are roosting together or in close proximity. The sensory basis for this discrimination is unknown, although olfaction is suspected. Another

TABLE 5. Results of chemosensory behavioral tests. For an explanation of the experimental design see text.

Stimulus	Locomotory response	Number responding (20 flies)
Host hair	weak positive	1
Host breath	none	0
Host faeces	none	0
Water washings of host	none	0
"OFF" (50%, N,N,-dimethyl-meta-toluamide)	strong negative	19

TABLE 6. Temperature preference of *Megistopoda aranea.* Positions of flies on a warmed glass plate were recorded with reference to substrate temperature after 20 minutes of free movement. A shielded 100-watt light bulb was the heat source. Air temperature was 18°C. Expected numbers of flies are based on relative areas of the substrate in each temperature range.

Temperature (°C)	No. of flies	Expected number
18-20	2	12
21-23	4	9
24-26	4	9
27-29	3	8
30-32	9	6
33-35	18	4
36-38	7	2

Observed distribution of flies by area does not fit the expected (random) distribution. ($P<.05$, Chi-square test.)

factor observed which may bear on these results is that *Carollia perspicillata, Glossophaga soricina,* and *Artibeus toltecus* are small bats and groom themselves more vigorously and frequently than do the larger *Artibeus jamaicensis* and *A. literatus*. Batflies, therefore, may have been groomed off by the more active hosts. The fur of the smaller bats is also shorter and may be more difficult for the batflies to grasp. Thus, the association of parasite and host could result from factors other than sensory orientation.

Similarly, the survival of *Megistopoda aranea* on various hosts may depend upon factors other than the nutritive requirements of the fly or the presence of phagostimulants. Of the bat species listed in Table 8, *Carollia* spp., *Glossophaga* sp., *Uroderma bilobatum* and *Stirnira* sp. did not adapt well to captivity. Individuals of these species showed signs of agitation and stress, did not adapt well to the diet provided, and had to be released after about a week if they were not to be kept as voucher specimens. Three *Artibeus cinereus* were kept with sheaths over hind claws, wings and mouth, and were forcefed for one week during which time two *M. aranea* were maintained on each without loss. It seems reasonable, therefore, that the survivorship of the bat fly on several hosts was dependent upon differences in host activities, including grooming.

Ecological Considerations

To the batfly the bat is both habitat and food, while the batfly causes a loss of

TABLE 7. Host species selection by *Megistopoda aranea*. Four flies were placed in each cage containing a male and female of two bat species. Host-selection of flies was recorded after one, two, and three days. Host-selection by sex was non-significant in each species. (*$P<.05$; Mann-Whitney-*U* test.)

Cage	Hosts	Day 2	Day 3	Day 4
I	*Artibeus jamaicensis*	1	3	1
	Artibeus literatus	3	1	3
II	*Artibeus jamaicensis**	4	4	3
	Carollia perspicillata	0	0	1
III	*Artibeus jamaicensis**	4	3	3
	Glossophaga soricina	0	1	1
IV	*Artibeus jamaicensis*	2	1	2
	Phyllostomus discolor	2	3	2
V	*Artibeus jamaicensis**	4	3	4
	Artibeus toltecus	0	1	0
VI	*Artibeus literatus**	3	4	4
	Carollia perspicillata	1	0	0

TABLE 8. Survival times of *Megistopoda aranea* on various hosts. Two flies were placed on each of three bats of each listed species. Each bat was kept separately in a fine wire-mesh cage and checked daily.

Host species	Number of flies surviving				
	Day 1	Day 2	Day 3	Day 4	Day 5
Artibeus j. jamaicensis	6	6	6	6	6
Artibeus literatus	6	6	6	6	6
Artibeus cinereus	6	5	2	2	1
Carollia perspicillata	6	4	1	0	0
Glossophaga soricina	6	5	5	5	5
Glossophaga sp.	6	4	0	0	0
Phyllostomus hastatus	6	6	6	4	4
Phyllostomus discolor	6	5	3	1	1
Uroderma bilobatum	6	4	3	3	3
Stirnira sp.	6	3	1	1	0

fitness to its host bat. The accommodations between hosts and parasites are paralleled on the level of their populations, for the relationship may be viewed as involving a population of parasites and a population of hosts, the properties of neither being fully derivable from the properties of individual hosts or parasites.

Although a single batfly can affect only one bat at a given time, it may parasitize several or even many host individuals during its lifetime. Table 9 shows the results of an inquiry into the ability of *M. aranea* adults to disperse from one bat to other bats in its colony. So rapid was this dispersal and redistribution that the bat colony must be considered the effective host unit for a batfly for any but the shortest time scale. It is, however, premature to conjecture about the effect of the presence of additional bats in the colony upon the immediate environmental conditions affecting the parasite since the effective microclimate of the batfly is not known, but speculation on the effect of host population densities or colony sizes on parasite incidence may now be fruitful. If, for example, the size of a colony governs its stability or the permanence of its roost in some manner, it would greatly influence the reproductive success of its associated batflies, which require bats to be present for emergent adults following pupation. Likewise, a larger colony may afford a batfly more opportunity to abandon a dying or unsuitable bat for a more suitable host.

The potential of *Megistopoda aranea* to transmit diseases would seem great. Sergent and Sergent reported the transmission of *Haemoproteus columbae* by the pigeonfly *Pseudolynchia maura,* a hippoboscid, in 1906 (Coatney, 1931); and O'Roke (1930) demonstrated that *Haemoproteus lophortyx,* a blood parasite of quail, is transmitted by another hippoboscid, *Lyn-*

TABLE 9. Host-to-host transfers of *Megistopoda aranea.* Ten flies were introduced onto one of five *Artibeus jamaicensis* (A) in each of five cages to determine how the flies would distribute themselves among the caged hosts. Flies were not marked in order to avoid possible injury. The incidence of the flies on each of the hosts was checked daily for five days.

Cage	Host	Day 1	Day 2	Day 3	Day 4	Day 5
I	A	10	8	5	2	2
	B	0	0	2	3	1
	C	0	0	0	1	1
	D	0	1	1	0	3
	E	0	0	0	2	1
II	A	10	6	3	2	3
	B	0	3	2	2	2
	C	0	0	1	2	1
	D	0	1	2	2	1
	E	0	0	0	0	0
III	A	10	3	3	0	1
	B	0	1	2	1	2
	C	0	1	0	1	2
	D	0	3	4	3	2
	E	0	2	0	4	1
IV	A	10	2	2	3	3
	B	0	1	2	1	2
	C	0	4	0	1	2
	D	0	2	0	2	1
	E	0	2	5	0	2
V	A	10	5	2	0	3
	B	0	0	1	5	3
	C	0	2	1	2	2
	D	0	0	4	1	0
	E	0	3	2	0	0

chia hirsuta. Transmission of this sort is more complex than the mechanical transmission required for the bacterial or viral diseases to which *Artibeus jamaicensis* is known to be susceptible. Moving from one host individual to another, *M. aranea* would appear to pose a threat to the health of *Artibeus* colonies if it serves as a vector for diseases of its hosts. Rabies may be spread as an aerosol, and investigations of the transmission of rabies in bats at the Trinidad Virus Laboratory did not implicate batflies as vectors (Greenhall, pers. comm.). One limitation to the vectorship-potential of *M. aranea* is its narrow host range, but further inquiry into this matter is warranted.

Artibeus jamaicensis is the host of other blood-sucking ectoparasites which would appear to compete with *Megistopoda aranea*. Other parasites collected on *A. jamaicensis* during the course of this investigation included three streblids, *Paratrichobius longicrus, Aspidoptera buscki,* and *Metelasmus pseudopterus,* and a spinturnicid mite, *Periglischrus iheringi*. Other parasites of *Artibeus jamaicensis* are reported by Wenzel et al. (1966). While these three other streblids, especially, could compete with *M. aranea,* other parasites did not exclude *M. aranea*. It would seem that *Artibeus* in Panamá has not been "saturated" with parasites and that populations of parasites of *Artibeus jamaicensis* are not at their maxima. Competition between ectoparasites would not be expected if their resources were not limiting.

If, however, a host bat is considered as a limited habitat, it is possible that populations of *Megistopoda aranea* are at their maxima and that competition between ectoparasitic species for space, rather than food, may occur. The potential maximum population would be a function of the host's behavioral tolerance for parasites, and parasites in excess of this limit would be removed by host grooming. The advantage under such pressures would lie with those parasites which could best avoid being dislodged. *M. aranea* is by far the most common ectoparasite of *A. jamaicensis* and presumably has this ability to a greater extent than do other parasites.

SUMMARY

Megistopoda aranea is the most frequent ectoparasite of *Artibeus jamaicensis* in Panamá where this study was conducted. *Artibeus literatus* is a much less frequent host. In spite of this, *M. aranea* is best considered as monoxenous, forming a stable system with its host. *Megistopoda aranea* disperses from host to host within a colony by direct transfer between adjacent hosts. The frequency distribution of flies on *Artibeus jamaicensis* resembles the expected Poisson distribution. The sexes of *Megistopoda aranea* are present in nearly equal numbers. Copulation is required for each reproduction. The larval stages last about 10 days in the body of the mother, and the pupal stage lasts about 23 days. The adult *Megistopoda aranea* lives several weeks. Breeding occurs throughout the year. The reproductive potential of the species seems to be limited by its viviparous habit. A description of the general and orientation behavior of *Megistopoda aranea* is given. Host-specificity of *Megistopoda aranea* may arise from ecological aspects of the host, rather than from the fly's sensory orientation.

RESUMEN

Megistopoda aranea es el ectoparásito más frecuente en *Artibeus jamaicensis* de Panamá. *Artibeus literatus* es un huésped de segundo orden, por su escasez. Por lo que *Artibeus jamaicensis* puede ser considerado como un huésped específico para *Megistopoda aranea*. El metodo de dispersión usado por *Megistopoda aranea* dentro de una colonia es por contacto directo entre los huéspedes. La distribucion de

frecuencia de *Artibeus jamaicensis* semeja la distribucion de Poisson. Hombras y machos de *Megistopoda aranea* se encuentran en igual número. Cada vez que se reproducen es necesaria la copulación. El estado larval dura 10 días dentro del cuerpo de la madre el estado pupal dura 23 días. Los adultos de *Megistopoda aranea* viven varias semanaś la reproducción se realiza durante todo el año. El potencial reproductivo de la especie parece estar limitado por sus modo vivíparo de reproducción. Descripción acerca de la conducta de *Megistopoda aranea* es incluida. La especificidad de *Megistopoda aranea* esta possiblemente más replacionada con la ecología del huésped que con la orientación sensorial del parásito hacia el huésped.

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